

# Biolocomotion without inertia

Saverio E. Spagnolie Department of Mathematics, UW-Madison Rishi R. Trivedi1, Rina Maeda1, Nicholas L. Abbott2, Saverio E. Spagnolie3, and Douglas B.

ShelleyFest 2019, Ann Arbor, MI Tutorial Session a complex patterned director field) over exceptionally long distances. Numerical simulations and analytical predictions for swimming speeds provide a mechanistic insight into the hydrodynamics of the system. This study lays the foundation for using



### Evolution of swimming strategies: Scale Matters.



*Escherichia coli*  D. Kunkel Microscopy



*Chlamydomonas*  D. Howard, UWLC



*Human spermatozoa*  D. Kunkel Microscopy



*Tracheal epithelium*  D. Kunkel Microscopy



*Spirochete*  W. Ellis, U. Belfast



*Paramecium*  A. Fleury, Orsay



*Volvox*  Warren Photography



*Mouse embryo nodal cilia*  S. Nonaka, NIBC, Japan



*Crystal Jellyfish*  Wikimedia commons



*Whale shark*  Georgia Aquarium



*Dragonfly*  Wikimedia commons



 *Barn Owl* Ron Dudley

### How do *you* swim?



Vandenberghe, Zhang, & Childress (2004).





**Alben** & Shelley, *PNAS*, 2005 Spagnolie, Moret, Shelley, & Zhang, *Phys. Fluids*, 2010 Ristroph & Childress, *J. Roy. Soc. Interface*, 2014

## Dynamic similarity: the Reynolds number



$$
\operatorname{Re}\left(\mathbf{u}_{t} + \mathbf{u} \cdot \nabla \mathbf{u}\right) = -\nabla p + \nabla^{2} \mathbf{u}
$$

$$
\nabla \cdot \mathbf{u} = 0
$$

$$
Re = \frac{\rho UL}{\mu} \quad \left(\frac{\text{inertial effects}}{\text{viscous effects}}\right)
$$



Real numbers

Re (St 
$$
\mathbf{u}_t + \mathbf{u} \cdot \nabla \mathbf{u}
$$
) =  $-\nabla p + \nabla^2 \mathbf{u}$   
\nRe =  $\frac{\rho UL}{\mu}$  St =  $\frac{L \omega}{U}$   
\nReynolds number  
\n $\omega \cdot \text{C}$ 

+ + + ( ) Oset force dipole force quadrupole Source dipole Rotlet dipole Figure 1. A swimming *E. coli* can be modeled at leading order as a Stokeslet dipole. At the next order, the flow in the far-field varies due to the length asymmetry between the backward-pushing *U*

At **zero** Reynolds number there is **no** inertia, and time is merely a parameter.

Stokes equations:

$$
\operatorname{Re}\left(\mathbf{u}_{t} + \mathbf{u} \cdot \nabla \mathbf{u}\right) = -\nabla p + \nabla^{2} \mathbf{u}
$$

$$
0 \qquad \nabla \cdot \mathbf{u} = 0
$$

Linearity + time-independence of the Stokes equations = kinematic reversibility: An instantaneous reversal of the forcing does not modify the flow patterns, only the direction in which they are occurring.



G.I. Taylor National Committee for Fluid Mechanics Films, 1961

Swimming strategies must respect fluid mechanics!

The Scallop Theorem

Life at Low Reynolds Number, E. M. Purcell, 1977







### Life at intermediate Reynolds number is *amazing*!





2 cm Shell-less pteropod mollusc *Clione antarctica* Childress & Dudley, (J. Fluid Mech. 2004)

An early mathematical model: "Taylor's swimming sheet" (Taylor, 1951)

$$
-\nabla p + \mu \nabla^2 \mathbf{u} = \mathbf{0}
$$
  $y = b \sin(kx - \omega t)$ 

FIG. 48. Taylor's swimming sheet model of swimming microorganisms.  $\gamma \gamma$ <sup>*y*</sup>  $\gamma$  *x y*  $\alpha$  *y*  $\alpha$  *y* Define a stream-function for the velocity:  $\mathbf{u} = \nabla^{\perp} \psi = (\psi_y, -\psi_x)$ 

$$
\Rightarrow \nabla^4 \psi = 0
$$

 $\mathbf{h}$ out small amplitude  $\varepsilon = \hbar k \ll 1$ . Expand about small amplitude  $\varepsilon = bk \ll 1$ = (*x, y, t*; ")*,* (453)

$$
\Psi(x, y, t; \varepsilon) = \psi^{(0)}(x, y, t) + \varepsilon \psi^{(1)}(x, y, t) + \varepsilon^2 \psi^{(2)}(x, y, t) + \dots,
$$
  

$$
U = U(\varepsilon) = U^{(0)} + \varepsilon U^{(1)} + \varepsilon^2 U^{(2)} + \dots
$$

*v*(*x, y* ! 1) = *V x*ˆ*,* (444) Solve Stokes equations order by order...

$$
U = \frac{1}{2} \frac{\omega}{k} \varepsilon^2 + O(\varepsilon^4) \approx \frac{1}{2} \omega k b^2 \quad \text{(Quiz: Why nothing at first order?)}
$$





What tools do we have? Lots.

Linear PDEs Green's functions Moment expansion / method of reflections / method of images Boundary integral representation Slender body theory Fast algorithms

.

.

.

Main points I want to highlight:

Physical ideas:

- 1. Kinematic reversibility / Scallop theorem
- 2. Quasi-static dynamics
- 3. Drag anisotropy of slender bodies
- 4. Stochastic (e.g. run-and-tumble) trajectories
- 5. Inside the flagellum: flagellin/polymorphism, microtubules/axoneme

Mathematical tools:

- 1. "Stokeslet" fundamental solution (Green's function) and its derivatives
- 2. A boundary-integral representation\*
- 3. Multipole expansion in the far-field: bacteria as force-dipoles.
- 4. Slender-body theory for thin filaments (flagella, cilia, etc.)

Dynamics are quasi-static. Swimming is essentially force/torque-free at any moment.



Scaling lengths, velocities on L, U as before, and scaling forces on  $\mu LU$ , we find

$$
\operatorname{Re}\left(\frac{m}{\rho V \Omega}\right) \left(\frac{V \sigma V}{L^3}\right) \ddot{\mathbf{x}}^* = \frac{1}{\mu UL} \mathbf{F}_{ext} + \int_{D^*} \mathbf{f}^* \, dS^*
$$

The body is in equilibrium at every moment. Even if **F**, **f** are changing in time. (Changes are slower than the viscous dissipation timescale.)

And if 
$$
|\mathbf{F}_{ext}|/(\mu UL) \ll 1
$$
, then  $\int_{D^*} \mathbf{f}^* dS^* = \mathbf{0}$ . Example: E. coli has  $|\mathbf{F}_g|/(\mu UL) \approx 10^{-2}$ 

### The torque-free constraint demands a counter-rotation



*Hydrodynamics of self-propulsion near a boundary* 111  $f(x)$ One answer: Don't worry about it! Taking the long view: mathematical modeling of swimming microbes via far-field hydrodynamics



the fluid flow far from a neutrally buoyant body The leading order approximation of the fluid flow far from a neutrally buoyant body

To be more precise let's develop some mathematical tools, starting with the most important one.

The "Stokeslet" fundamental solution (Green's function) is the key to everything.

What to do to a linear PDE? 
$$
-\nabla p + \mu \nabla \cdot \mathbf{u} + \mathbf{f} \delta(\mathbf{x}_0) = \mathbf{0}
$$
  
\n**Poke it.**  $\nabla \cdot \mathbf{u} = 0$ 

 $\mathbf{u}(\mathbf{x}) = \frac{1}{2}$  $8\pi\mu$ By linearity, we must have  $\mathbf{u}(\mathbf{x}) = \frac{1}{8\pi n} \mathbf{G}(\mathbf{x} - \mathbf{x}_0) \cdot \mathbf{f}$   $p(\mathbf{x}) = \frac{1}{8\pi n}$  $8\pi$  ${\bf \Pi}({\bf x} - {\bf x}_0) \cdot {\bf f}$ 

Solving (e.g. by Fourier transform and inversion),



Read Pozrikidis (1992)

Derivatives of the Stokeslet are also solutions to the Stokes equations.

Linear PDE —> Linear combinations of Stokeslets also solve the primary equations

This includes derivatives (as differentiation is a linear operation)

$$
\mathbf{u} = \frac{1}{d} \left( \mathbf{G} (\mathbf{x} - d\mathbf{\hat{x}}) \cdot \mathbf{f} - \mathbf{G} (\mathbf{x}) \cdot \mathbf{f} \right) \rightarrow \mathbf{\hat{x}} \cdot \nabla_{\mathbf{x}_0} (\mathbf{G} \cdot \mathbf{f})
$$

is a solution, too.

K

"Stokeslet dipole" or "force dipole"





How else can we poke the system?

$$
-\nabla p_0 + \mu \nabla^2 \mathbf{u}_0 = \mathbf{0}
$$

$$
\nabla \cdot \mathbf{u}_0 + M \delta(\mathbf{x}) = 0
$$

$$
\mathbf{u}_0 = \frac{-M\mathbf{x}}{4\pi |\mathbf{x}|^2}, \ \ p_0 = 0
$$
<sub>Source/sink</sub>

Including… all potential flow solutions

Since 
$$
\nabla^2 \mathbf{u}_0 = \mathbf{0}
$$
,  $p_0 = 0$ 

… all "potential flow" solutions (from infinite Reynolds number flow!) also solve the Stokes equations (zero Reynolds number flow!)

$$
\mathbf{e}\cdot\nabla\mathbf{u}_0=\frac{1}{|\mathbf{x}|^3}\left(-\mathbf{I}+\frac{3\mathbf{x}\mathbf{x}}{|\mathbf{x}|^2}\right)\cdot\mathbf{e}=\mathbf{D}(\mathbf{x})\cdot\mathbf{e}
$$

Source dipole/doublet  $P<sub>1</sub>$ 



The flow due to a moving sphere is simply represented by a combination of singular solutions

(!) A particularly interesting combination:

$$
\mathbf{u} = \left(\mathbf{G} - \frac{a^2}{3}\mathbf{D}\right) \cdot \frac{\mathbf{F}}{8\pi\mu}
$$



has  $\mathbf{u}(r=a) = \frac{1}{c}$ , **constant!** Call it **U**. Then F  $6\pi\mu a$ *,*

$$
{\bf F}_{fluid}=-6\pi\mu a{\bf U}
$$

*(Stokes Drag Law)*

A more general multipole expansion often starts with a boundary integral representation *Hydrodynamics of self-propulsion near a boundary* 5

$$
8\pi\mu \mathbf{u}(\mathbf{x}) = -\int_{\partial D} \mathbf{G}(\mathbf{x} - \mathbf{y}) \cdot \mathbf{f}(\mathbf{y}) dS_y \quad \text{for } \mathbf{0} \quad \text{or} \quad \mathbf{0}
$$
  

$$
\mathbf{G}_{ij}(\mathbf{x}, \mathbf{y}) = \frac{1}{|\mathbf{x} - \mathbf{y}|} + \frac{(x - y)_i(x - y)_j}{|\mathbf{x} - \mathbf{y}|^3}
$$

 $\frac{1}{2}$ (Not the most general form… stay tuned for Shravan's lecture!)

Now consider the flow at a point **x** far from the body.

Expanding around **0**,

$$
\mathbf{G}(\mathbf{x} - \mathbf{y}) = \mathbf{G}(\mathbf{x} - \mathbf{0}) + \mathbf{y} \cdot \nabla_y \mathbf{G}(\mathbf{x}) + \frac{1}{2} \mathbf{y} \mathbf{y} : \nabla \nabla \mathbf{G}(\mathbf{x}) + \dots
$$

So

$$
8\pi\mu\,\mathbf{u}(\mathbf{x}) = \int_{\partial D} \left[ \mathbf{G}(\mathbf{x}-\mathbf{0}) + \mathbf{y}\cdot\nabla_y \mathbf{G}(\mathbf{x}) + \frac{1}{2}\mathbf{y}\mathbf{y}:\nabla\nabla\mathbf{G}(\mathbf{x}) + \dots \right] \cdot \mathbf{f}(\mathbf{y})dS_y
$$

u(x)  $\mathbf{e}^{\mathbf{X}}$ 

 $\mathbf{X}$ 

## Multipole expansion

$$
8\pi\mu u_i(\mathbf{x}) = G_{ij}(\mathbf{x})F_j + \partial_k G_{ij}(\mathbf{y})S_{kj} + \partial_m \partial_k G_{ij}(\mathbf{x})M_{mkj} + \dots
$$

$$
\mathbf{F} = \int_{\partial D} \mathbf{f}(\mathbf{y}) dS_y \qquad \mathbf{S} = \int_{\partial D} \mathbf{y} \mathbf{f}(\mathbf{y}) dS_y \qquad \mathbf{M} = \frac{1}{2} \int_{\partial D} \mathbf{y} \mathbf{y} \mathbf{f}(\mathbf{y}) dS_y
$$

$$
= \mathbf{F}_{ext}
$$

or  

$$
\mathbf{u}(\mathbf{x}) = \frac{1}{8\pi\mu} \mathbf{G}(\mathbf{x}) \cdot \mathbf{F} + \frac{1}{8\pi\mu} \nabla_y \mathbf{G}(\mathbf{x}) : \mathbf{S} + \dots
$$

The pusher and puller business

Neutrally-buoyant?

\n
$$
\mathbf{F} = \mathbf{F}_{\text{ext}} = \mathbf{0}
$$
\nAxisymmetric?

\n
$$
\mathbf{S} = -\sigma \mathbf{p} \qquad \qquad \ulcorner \left( \begin{array}{c} \text{S} \\ \text{A} \end{array} \right)
$$
\nAxisymmetric?

\n
$$
\mathbf{S} = -\sigma \mathbf{p} \qquad \qquad \ulcorner \left( \begin{array}{c} \text{S} \\ \text{S} \end{array} \right)
$$
\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p} \mathbf{p} = \frac{-\sigma}{8\pi\mu} \mathbf{p} \cdot \nabla\_y (\mathbf{G}(x) \cdot \mathbf{p})\nu(x) = \frac{-\sigma}{8\pi\mu} \nabla\_y \mathbf{G}(x) : \mathbf{p

(Stay tuned for Becca/David's lectures!) flagellum and counter-rotation of the counterof the Stokeslet quadrupole component of spectrup component of spectrum  $\mathcal{C}(\mathcal{C})$ ctures!) of tures!) ctures!)  $\frac{1}{2}$  More details enter as you approach the body

At a distance, a (phase-averaged) axisymmetric organism's far-field representation is:



This useful perspective provides insight into many phenomena. For example… How does a wall affect the swimming trajectory? Use classical ideas from E&M…



Method of images / Method of reflections

Stokeslet image (Blake 1971) Stokeslet Stokeslet image

Zero velocity on the wall

### See also: Faxén's Law, **Lorentz reflection theorem**

Computational interlude: bc

$$
8\pi\mu\,\mathbf{u}(\mathbf{x}) = \int_D \mathbf{G}(\mathbf{x})
$$



$$
\mathbf{G}_{ij}(\mathbf{x}, \mathbf{y}) = \frac{1}{|\mathbf{x} - \mathbf{y}|} + \frac{(x - y)_i (x - y)_j}{|\mathbf{x} - \mathbf{y}|^3}
$$

$$
\mathbf{T}(\mathbf{x}, \mathbf{y}) = -6 \frac{(\mathbf{x} - \mathbf{y})(\mathbf{x} - \mathbf{y})(\mathbf{x} - \mathbf{y})}{R^5}
$$

"Stresslet" singularity





$$
\mathbf{G}_{ij}(\mathbf{x}, \mathbf{y}) = \frac{1}{|\mathbf{x} - \mathbf{y}|} + \frac{(x - y)_i (x - y)_j}{|\mathbf{x} - \mathbf{y}|^3}
$$

$$
\mathbf{T}(\mathbf{x}, \mathbf{y}) = -6 \frac{(\mathbf{x} - \mathbf{y})(\mathbf{x} - \mathbf{y})}{\mathbf{T}(\mathbf{x} - \mathbf{y})}
$$

"Stresslet" singularity  $\hat{z}$ 

Figure 3. A model swimmer near a wall. The body swimmer near a wall. The body swims in a direction e, which may be decomposed into a horizontal part along  $\mathcal{N}$  and a vertical part along  $\mathcal{N}$ . The pitching angle  $\mathcal{N}$ Gimbutas, L. Greengard, S. Veerapaneni, (2015) - Papkovich-Neuber potential  $\partial \theta$  denotes the denotes the angle of the horizontal system  $\partial \theta$  $\rho_{\text{ref}}$  and  $\rho_{\text{ref}}$  and the pitching in  $\rho_{\text{ref}}$  decoupled from the pitching and height dynamics of  $\rho_{\text{ref}}$ Mitchell & Spagnolie, J. Comput. Phys. (2017) - Lorentz reflection theorem Spagnolie & Lauga (2012) - Brute force

$$
\mathcal{T}_{ijk}^*(\bm{x},\bm{y}^*) = \frac{6\hat{X}_iX_jX_k}{|\bm{X}|^5} + 12x_3\frac{\beta_{ik}y_3X_j + \beta_{ij}y_3X_k - \delta_{jk}x_3\beta_{i\ell}X_{\ell}}{|\bm{X}|^5} - 60x_3y_3\beta_{i\ell}\frac{X_jX_kX_{\ell}}{|\bm{X}|^7},
$$

 $\mathbf{v}$  is the unit normal vector pointing into the fluid,  $\mathbf{v}$  is an integration variable variable

 $\hat{\mathbf{z}}$ 

 $\hat{\textbf{x}}$ 

 $\mathbf{\hat{y}}$ 

(*x y*)(*x y*)(*x y*)

 $\phi$ 

 $\sum_{k=1}^{n}$ 

 $D^*$ 

 $h$   $\left| \frac{h}{h} \right| \leq k$ 

*D*

 $\theta$ 

 $-$  **FF** 

e

## Comparing to full numerical simulations, analytical predictions are confirmed for all but the closest of wall-interactions 82



#### tal axis is the *y*-direction. The lateral movements are plotted to scale, while the movements in ration is very accurate. Animation purposes  $\mathbf x$ The far-field approximation is very accurate.

$$
\mu/\mu_0 = 1 + \frac{5}{2}c + 7.6\epsilon^2 \quad 6.95c^2 \text{ (Yoon & Kim, '87)}
$$

Batchelor & Green, J. Fluid Mech. (1972)

Mitchell & Spagnolie I Fluid Mech 201 Mitchell & Spagnolie, J. Fluid Mech. 2015 Mitchell & Spagnolie, J. Comput. Phys. 2017  $\mathbf{1}$  direction at the point farther point farther probability farther probability farther point farther p

What is the effect of a nearby boundary on swimming trajectories?

> $s \in \mathbb{Z}$  becomes equations. if different functional forms are used, the linear model is  $\bullet$   $\bullet$   $\bullet$ **ARTICLES**

Paxton et al., (JACS, 2004). et al., (JACS, 2004) Paxton et al., (JACS, 2004 by solving the convection-diffusion eq 1:

Takagi et al. (20  $\mathcal{D}$  $\left\{\frac{1}{2}\right\}$ Takagi et al. (2013)





Spagnolie et al.  $(2015)$  $S$ pagnone et al. (2019) But don't lose sight of reality…



Chlamydomonas swimming near a surface

Kantsler et al. (PNAS 2012).









CC-2347 shf1



CC-2679 mbo1

### For more details you need… more tools!

A Singularty method  $I_n$  "the singularity method" we try to find distributions of singularities<br>internal to a body to satisfy no-slip,  $(\vec{v}|_{3D} = \vec{V} + \vec{J} \vec{Q} \times \vec{x})$ Prolate ellipsoid: Ly (7777)  $Chwang + Wu \frac{v}{ar}2^{s}(1975)$  $\vec{v} = \int_{-c}^{c} \omega_1 \underline{G} \cdot \hat{x} + \omega_2 \underline{G} \cdot \hat{y} ds + \int_{-c}^{c} (c^2 - s^3) \underline{G} \beta_1 \underline{D} \cdot \hat{x} + \beta_2 \underline{D} \cdot \hat{y} ds$ Rotation, and linear backgound Flows (shear/extensional) are done there too.

But that only gets us so far. How would we try to model this one?

 $\frac{1}{2}$  $\partial D$ 

Method 1: Compute.

Coming soon! Be patient!

There are numerous numerical approaches

- Boundary integral methods
- Method of "Regularized Stokeslets"
- Various "immersed boundary methods"

Method 2: Exploit small parameters. For instance, the aspect ratio of the flagellum.

First let's back up and talk about drag anisotropy.

The sedimentation speed of a sphere in a **viscous** fluid is linear in its surface area

$$
F_g = \left(\frac{4}{3}\pi a^3\right) \Delta \rho g \int \int a \int F_{Drag} = 6\pi \mu a U
$$
  
"Stokes drag"

$$
0 = F_g + F_{Drag}
$$

$$
U = \frac{2a^2}{9\mu} \Delta \rho g
$$

Hydrodynamic interactions increase the speed of multiple spheres in Stokes flow

$$
g \downarrow \downarrow \downarrow \qquad \qquad \qquad \qquad \qquad \boxed{a}
$$
\n
$$
U = \frac{2a^2}{9\mu} \Delta \rho g \left(1 + \frac{3a}{4L}\right) + O\left(\frac{a^2}{L^2}\right) \qquad \text{(far-field expansion)}
$$
\n
$$
\frac{3a}{2L} \bigodot \bigdownarrow g
$$

(Torque balance also induces a rotation)

$$
\Omega = \frac{a^3}{12\mu L^2} \Delta \rho g + O\left(\frac{a^3}{L^3}\right)
$$

Hydrodynamic interactions lead to **drag anisotropy** of slender filaments

$$
\mathbf{F}_g = \begin{bmatrix} \xi_{||} \hat{\mathbf{s}} \hat{\mathbf{s}} + \xi_{\perp} (\mathbf{I} - \hat{\mathbf{s}} \hat{\mathbf{s}}) \end{bmatrix} \cdot \mathbf{U} \begin{bmatrix} \xi_{\perp} \\ \xi_{||} \\ \xi_{||} \end{bmatrix} \approx 2
$$
  
Filament aspect ratio  $\varepsilon \ll 1$ 

Hydrodynamic interactions lead to **drag anisotropy** of slender filaments



$$
\mathbf{F}_g = \left[\xi_{||}\mathbf{\hat{s}}\mathbf{\hat{s}} + \xi_{\perp}(\mathbf{I} - \mathbf{\hat{s}}\mathbf{\hat{s}})\right] \cdot \mathbf{U}
$$

How to swim at zero Reynolds number: drag anisotropy  $\frac{1}{2}$  of type  $\frac{1}{2}$  cells. The model presented here uses some simplifying assumptions, and leaves a number of open  $\mathbf{r}$ 



$$
\mathbf{F}_g = \begin{bmatrix} \xi_{||} \hat{\mathbf{s}} \hat{\mathbf{s}} + \xi_{\perp} (\mathbf{I} - \hat{\mathbf{s}} \hat{\mathbf{s}}) \end{bmatrix} \cdot \mathbf{U} \quad \frac{\xi_{\perp}}{\xi_{||}} \approx 2
$$

Filament aspect ratio  $\varepsilon \lll 1$ 

component which counters the retarding the retarding the retarding the form of Theory" This is the basis of "Resistive Force Theory" considered by other authors, and the degree and the degree and the degeneracy mentioned above  $\alpha$ 



Gray & Hancock, (J. Exp. Biol. 1955)



**Sea-urchin** *Lytechinus* spermatozoon **C.J. Brokaw, Caltech** 

A first pass at slender filament hydrodynamics: resistive force theory



Pros: simple! Cons: Error is O(1). Great so long as  $|\log \varepsilon| \gg 1$ , or  $\varepsilon \ll 10^{-10}$ !

Stepping up the accuracy: slender-body theory (matched asymptotics, relates to the singularity method) matched asymptotics, relates to the singularity method)

$$
\epsilon = \frac{a}{L} \ll 1 \longrightarrow \mathbf{K}[\mathbf{f}] - \mathbf{K}[\mathbf{f}] + (\epsilon^2 \log(\epsilon)) \qquad \mathbf{\hat{s}} = \mathbf{x}_s
$$
\nLocal operator \nNonlocal integral operator\nwhere\n
$$
\Lambda[\mathbf{f}] = [(c(s) + 1)\mathbf{I} + (c(s) - 3)\hat{\mathbf{s}}(s)\hat{\mathbf{s}}(s)] \cdot \mathbf{f}(s)
$$
\n
$$
\mathbf{K}[\mathbf{f}](s) = \int_0^1 \left( \frac{\mathbf{I} + \hat{\mathbf{R}}(s, s')\hat{\mathbf{R}}(s, s')}{|\mathbf{R}(s, s')|} \cdot \mathbf{f}(s') - \frac{\mathbf{I} + \hat{\mathbf{s}}(s)\hat{\mathbf{s}}(s)}{|s - s'|} \cdot \mathbf{f}(s) \right) ds',
$$
\n
$$
c(s) = \log \left( \frac{4s(1 - s)}{\epsilon^2 r(s)^2} \right)
$$
\nSpecial profile:

$$
r(s) = \sqrt{4s(1-s)}
$$

SBT is often the basis for high-accuracy  $\int^L \mathcal{L}$  $\therefore$   $\therefore$  and sometimes analysis (small amplitude)

$$
\int_0^L \frac{\mathcal{L}_p(s') - \mathcal{L}_p(s)}{|s' - s|} ds' = \lambda_p \mathcal{L}_p(s)
$$

 $s'$ 

soluculus analysis (sinali amplitude) (diagonalized by Legendre polynomials)

#### Health warning: dealt Healt<sup></sup>



#### What's **f** ?  $\sum_{\alpha}$  $Wh$  $\ddot{\text{P}}$

Depends. Might be just like in the RFT calculation. i.e. Rigid body dynamics assumed, use net-force on the body to infer  $\mathbf{f}(s)$ , but now via SBT.  $\overline{\mathbf{D}}$  $\lim_{\epsilon \to 0} \frac{1}{\epsilon}$ for a flagellum and the results of  $\mathbf{b}$ u  $f_{\text{obs}}$  Might because theory of Gray and resistive force theory  $f_{\text{obs}}$  $\frac{1}{2}$  $\frac{1}{1}$  $\mathcal{L}$ of Lighthill (2) (data blue lines). The regularized Stockesler theory and regularized Stockesler theory and stockes  $ST_{\text{e}}$  and substitutions both rely on the linearity of the linear  $t \perp$  calculation.  $t_0$  and for  $\cos$  and the location reference se net-force on the body to infer  $\mathbf{r}\mathrm{(s)}$ 

But a richer class of problems links the local viscous traction to internal stresses in a continuously deformable filament. 75 represent the fluid response to the fluid response to the fluid response to the fluid response to the fluid re<br>
response to the fluid  $\begin{bmatrix} 1 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$   $\begin{bmatrix} 1 & 1 & 0 \\ 0 & 1 & 1 \end{bmatrix}$   $\begin{bmatrix} 2 & 1 & 0 \\ 0 & 1 & 1 \end{bmatrix}$ where John is the Oseen tensor, and the Oseen tensor, and the Oseen tensor, and the Oseen tensor, and the Osee  $lam$ s trat<br>ent. rcuon



Perhaps the force per unit length on the filament is found by the principal of virtual work. Quick example…

An inextensible Euler-Bernoulli beam (small deflections)

$$
\mathcal{E} = \frac{B}{2} \int_0^L |\mathbf{x}_{ss}|^2 ds + \int_0^L \frac{T(s)}{2} (|\mathbf{x}_s| - 1)^2 ds
$$

Dimensionless viscous drag:

$$
\mathbf{f}(s) = -\mathbf{F}_g(s) - (T(s)\mathbf{x}_s)_s + \beta(B(s)\mathbf{x}_{ss})_{ss}
$$
  
Viscous Gravity Tension Elasticity  
drag  
 $\beta \gg 1$ : Stiff filaments (rods)  
 $\beta \ll 1$ : Floppy filaments

s = 0  
\n
$$
a \cdot r(s)
$$
  
\n**x**(s)  
\n  
\n $d s$   
\n $s = L$ 

Weakly flexible filaments sedimenting under gravity: shapes and trajectories slowly approach equilibrium



Xu & Nadim (1992) Li et al. (2013) Manikantan et al. (2014)

### Eukaryotic vs. prokaryotic flagella: elastohydrodynamics



Planar waves (eukaryotic flagella) must be driven actively along the entire filament



(Ann. Rev. Fluid Mech 1977)

#### is given by the integrated curvature and integrated curvature along the integration of the film *2.2. Enthalpy functional* constraint in the arcle of the internal force density  $\alpha$  is the arcle of the arcle of the internal force density  $\alpha$  is the arcle of the arcle of the arcle of the inte to the sliding displacement ∆ as described by the contribution ! d*s f*∆. The variation of this term <sup>=</sup> <sup>∂</sup>*s*[(κ*C*˙ <sup>−</sup> *af*)*<sup>n</sup>* <sup>−</sup> <sup>τ</sup> *<sup>t</sup>*]*.* (11) under small deformations of the filament shape represents the internal fluid for interna δ*G* **B. Fluid-body interactions** The fluid-body interactions are modelling the local structure. resistive force theory of Gray and Hancock !1955". 79 R

(*a*) Nexin Membrane Outer dynein arm Inner dynein arm Central singlet microtubules (*b*) Microtubule doublet where the normalized tangent vector  $\left(\begin{matrix} a \ b \end{matrix}\right)$   $\left(\begin{matrix} b \ c \end{matrix}\right)$   $\left(\begin{matrix} c \ c \end{matrix}\right)$  $\left[\begin{matrix} 0 & 1 \\ 0 & 0 \end{matrix}\right]$   $\left[\begin{matrix} 0 & 1 \\ 0 & 0 \end{matrix}\right]$   $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left[\begin{matrix} 0 & 0 \\ 0 & 0 \end{matrix}\right]$  $\left$ **2.1. Bending and sliding and** 

#### **Generic aspects of axonemal beating**  $\mathbf{R}_{\text{standard Spokes}}$  characterizes  $\mathbf{S}_{\text{linear singlet}}$  $\alpha$  defier to aspects of axofiental beating  $\overline{\text{BD}}$ d*s* ts **or axonem** Λ **ic aspects of axonemal beating** into tangential and normal components, as is the correspond-

### **Sébastien Camalet and Frank Jülicher Manuel Andrew Sébastien Camalet and Frank Jülicher**

PhysicoChimie Curie, UMR CNRS/IC 168, 26 rue d'Ulm, 75248 Paris Cedex 05, France Cedex 05, France<br>E-mail: scamalet@curie.fr and julicher@curie.fr  $\sqrt{\frac{f(s)}{f(s)}}$ cuno,<br>ce *s* d*s*′ δ*G/*δ*r* + *F*ext(*L*) = !*KT* − *KN*"**s***ˆ*!**s***ˆ* · **u**" + *KN***u**. !6" m

*New Journal of Physics* **2** (2000) 24.1–24.23 (http://www.njp.org/) Received 7 June 2000; online 4 October 2000  $s$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{1}{s}$   $\frac{s}{s}$   $\frac$ W*ew Journal of Physics* 2 (2000) 24.1–24.23 (http://www.njp.org/). The end which satisfies (2000) 24.1–24.23 (http://www.njp.org/). The end which satisfaction of the end of the end which satisfaction of the end of the end  $t_{\text{t}}$  the integration of the integrated forces acting on the filament. The filament action action on the filament.  $(0)$  24.1.24.23 (bttp:// $_{\text{turb}}$ .exx/  $\frac{1}{2}$  directly  $\frac{1}{2}$  ( $\frac{1}{2}$  and  $\frac{1}{2}$ 

characterizes the general physical mechanisms that govern that govern that govern that govern the behaviour of<br>Characterizes that govern the behaviour of behaviour of behaviour of behaviour of behaviour of behaviour of be

$$
G \equiv \int_0^L \left[ \frac{B}{2} C^2 + f \Delta + \frac{\Lambda}{2} \dot{r}^2 \right] ds. \quad (C = \kappa)
$$
  

$$
\Delta = a \int_0^s ds' C
$$





and the local fluid fluid is the local fluid by the assumption of the assumption of a state  $\alpha$ 

1 and 50 *µ*m. We discuss the effects of the boundary conditions and externally **Figure 8.** Oscillation frequency  $\omega_c/2\pi$  at the bifurcation point effectively as an elastic rod lead to local sliding displacements of this rod lead to local sliding displacements of this rod lead to local sliding displacements of this rod lead to local sliding displacements. In this ro **Figure 8.** Oscillation frequency  $\omega_c/2\pi$  at the **Figure 8.** Oscillation frequency  $\omega_c/2\pi$  at the bifurcation point

the local flagellum curvature &!*s*,*t*" using the classical elastic

**2. Internally driven filament**

### Shape matters: viscous dissipation vs bending costs



Spagnolie & Lauga, (Phys. Fluids 2009)

### Most **bacteria** swim by rotating a slender, helical flagellum / many helical flagella.

Helical waves (prokaryotic flagella): rotation of a solid helix leads to locomotion



**Rhodobacter sphaeroides**  H. C. Berg, Harvard

Most **bacteria** swim by rotating a slender, helical flagellum / many helical flagella. *Salmonella* and *E. coli* are "peritrichous" (many flagella)...



flagellar filament. The contract for graphing to  $\mathbf{1}$ ...and exhibit *run* and *tumble* locomotion:



Berg Lab, Harvard  $\mathcal{A}$ 



1997) Namba & Vonderviszt, Quart. Rev. Biophys. (1997) Turner, Ryu & Berg, J. Bacteriol. (2000)  $\frac{1}{2}$  of the intervals were normal. However, if they were not if

But keep an eye on reality! For instance, CW and CCW rotations yield different behavior Polymerized Flagellin protein micro-structure is not symmetric... external tions between neighboring subunits within a protofilament are necessary to ensure the uniqueness of helical well potential for twist, due to lateral interactions between neighboring protofilaments. Cooperative interac- is intermediate between the two spacings favored by the double-well potential. The second switch is a double $a$  $\frac{di\hat{f}}{dt}$ ifferd<br>- tions in response to the binding of the binding o<br>- the binding of the binding  $\mathbf d$ negative feedback control of the DNA-binding *trp* repressor in *Escherichia coli* yiel aspar- tate transcarbamoylase, also in *E. coli*  $\sqrt{ }$ W rotations y<br>ymmetric...  $\int$  and CCV r<br>yi  $\frac{1}{2}$ CC<br>binding formation<br>of syre compared the conformation<br>is the conformation subset of a new subset of <br>is not a new subset of a new subset of a new subset of a new subset of a new subset o  $\frac{1}{2}$  $W<sub>i</sub>$ <br>ure  $, C$  $C<sup>1</sup>$  $\ddot{=}$  $\frac{1}{2}$  $\frac{1}{\sqrt{2}}$ ance<br>o-str  $\mathfrak{t}$ de subter in the subter of the substitution of the substitution of the substitution of the substitution of the<br>  $\frac{1}{2}$  of the substitution of the substitution of the substitution of the substitution of the substitution<br>  $\overline{a}$  shortsubunits shape arises when some of the protofilaments consist of only around each other to form the filament, a helical filament may be grouped into 11 protofilaments which slowly wind y  $\overline{O}$  $\overline{\text{li}}$ fila- *E. coli* is left-handed with a pitch of 2.5 lin e<br>a diameter of 0.44<br>a diameter of 0.44  $\mathbf r$ e<br>po ton<br>agell



Asakura, Adv. Biophys. (1970) Calladine, J. Mol. Biol. (1978) Hasegawa et al., Biophys. J. (1998) Srigiriraju & Powers, Phys. Rev. E (2006)  $\begin{pmatrix} 1 & 0 & \pm 0 \\ 0 & 0 & 0 \end{pmatrix}$  $\Lambda$ sakura, Adv. Biophys. (1970) J.  $(1990)$ repeat distances of strand joints, a relatively large negative subunits are labeled **A** and **B** and  $\mathbf{H}_{\text{average}}$  interaction represents the  $\mathbf{R}_{\text{total}}$ distances between the red and blue sites and plus  $\mathcal{O}$  is  $\mathcal{O}$  and  $\mathcal{O}$  and  $\mathcal{O}$  is the L-type than the L-type



Experimental observations indicate a circular relationship in the pitch-circumference plane



Are biological fluids any different?

Biolocomotion in viscoelastic fluids

Biological fluids are often host to a polymeric microstructure

In flow: viscous stresses compete with entropic contraction of polymers

Helical bacteria *Leptospira (Leptosprosis)* and *B. burgdorferi (Lyme disease)*  swim faster...





Berg & Turner, 1979; Spielman & Kimsey, 1990



### Biolocomotion in viscoelastic fluids

Biological fluids are often host to a polymeric microstructure

In flow: viscous stresses compete with entropic contraction of polymers

...while *C. elegans* swims slower...  $\mathcal{P}_\text{R}$ 



Lauga, *Phys. Fluids*, 2007 Teran, Fauci & Shelley, *Phys. Rev. Lett.*, 2010 Shen & Arratia, *Phys. Rev. Lett.*, 2011  $\frac{1}{200}$   $\frac{1}{90}$   $\frac{1}{90}$   $\frac{1}{90}$   $\frac{1}{200}$  $\frac{d}{dt}$  definition speed decreases as elasticity,  $\frac{d}{dt}$  is  $\frac{d}{dt}$  in  $\frac{d}{dt}$  in  $\frac{d}{dt}$  is  $\frac{d}{dt}$  in  $\frac{d}{dt}$ 

A new dimensionless number appears:

Deborah number: De =  $\lambda_1 \omega$ 

Free historical notes:

Proposed by Markus Reiner (Technion) (1920): "The mountains flowed before the Lord" (Deborah; Judges 5:5)

Also coined the term: "rheology" w/ Bingham (study of deformation/flow of matter) Inspired by the *aphorism of Simplicius:* "panta rhei" (*Everything flows*)

What tools do we have?

Linear PDEs Green's functions Moment expansion / method of reflections / method of images Boundary integral representation Slender body theory

…

What tools do we have?



Fluid memory… and worse

Coupled nonlinear time-dependent PDEs… with moving immersed boundaries! e.g. Stokes/Oldroyd-B:

$$
\nabla p = \eta_s \nabla^2 \mathbf{v} + \nabla \cdot \boldsymbol{\tau}^p \qquad \nabla \cdot \mathbf{v} = 0
$$

$$
\boldsymbol{\tau}^p+\lambda_1\overline{\boldsymbol{\tau}}^p=\eta_p\dot{\boldsymbol{\gamma}}\qquad\overline{\boldsymbol{\tau}}=\frac{\partial\boldsymbol{\tau}}{\partial t}+\mathbf{u}\cdot\nabla\boldsymbol{\tau}-\boldsymbol{\tau}\cdot\nabla\mathbf{u}-\nabla\mathbf{u}^T\cdot\boldsymbol{\tau}
$$

Separation of time-scales Finite-time blow up, "high-Weissenberg number catastrophe", …

**(i.e. Pray for a small parameter/symmetry** *and* **start computin')**

Swimming of a 2D sheet in a viscoelastic fluid (Lauga, *Phys. Fluids*, 2007)

$$
y = b \sin(kx - \omega t)
$$

Stokes/Oldroyd-B:

okes/Oldroyd-B: 
$$
\nabla p = \nabla \cdot \tau \nabla \cdot \mathbf{v} = 0 \qquad \tau = \tau_0 + \epsilon \tau_1 + ...
$$

Small-amplitude asymptotics: 
$$
\frac{U}{U_N} = \frac{1 + (\eta_s/\eta)De^2}{1 + De^2} \qquad \text{De} = \lambda_1 \omega
$$

$$
\eta = \eta_s + \eta_p
$$

Identical swimming speeds for: FENE-P, Johnson-Segalman-Oldroyd, Giesekus *x*  $\frac{1}{2}$   $\frac{1}{2}$ *r*, Johnson-Segalman-Oldroyd, Giesekus

Reciprocal theorem extensions (finite bodies, etc.): Elfring & Lauga, (2015)

The results can be generalized for a wider class of helical bodies/waves The results can be generalized for a wider class of helical bodies/waves

The results can be generalized for a water class of internal bodies, waves  
\n
$$
\tau_1 + \frac{\text{De}}{v} \left( \frac{\partial}{\partial \zeta} - v \frac{\partial}{\partial \theta} \right) \tau_1 = \dot{\gamma}_1 + \frac{\beta \text{De}}{v} \left( \frac{\partial}{\partial \zeta} - v \frac{\partial}{\partial \theta} \right) \dot{\gamma}_1
$$
\n
$$
\dot{\gamma}_1 = \sum_k \dot{\gamma}_1^{(k)} \exp(ik\theta).
$$
\n
$$
\tau_1^{(k)} = \eta^*(k) \dot{\gamma}_1^{(k)}
$$

complex viscosity 
$$
\eta^*(k) = (1 - ik\beta \text{De})/(1 - ik\text{De})
$$

 $\beta = \eta_s/\eta$ 

 $/2$ 

stresses on µ!. The dimensionless swimming speed and rigid body rotation rate are written as *U* =  $\frac{Z_{\Box}}{Z_{\Box}}$ /!, the cylindrical tube has dimensionless radius *L* = *L*⇤ ⌫⇤*A*. All variables are henceforth understood to be dimensionless unless otherwise stated. Since time does not appear in the Stokes equations, the flow is solved without loss of generality at *t* = 0 and we omit the  $\frac{1}{\sqrt{2\pi}}$ Application of the same non-dimensionalization  $\mathbb{R}^n$ is force- and torque-free in the zero Reynolds number limit. For neutrally buoyant organisms, the  $S(\mathcal{Y}, \mathcal{Y})$  is the free of a net hydrodynamic force or to the  $\mathcal{Y}$ torque-free condition, for example, is that organisms such as *Paramecium* and *Volvox* for which metacheronal ciliary waves pass along the surface at angle  $|k|$  $\mathbf{I}$  in the opposite direction as the opposite direction as we will show  $\mathbf{I}$ In this work, we will make use of a helical coordinate system, (*r*, ✓, ⇣), denoting a point in space  $\frac{1}{x}$   $\frac{0}{x}$   $\frac{1}{z}$ complex viscosity governs the stored elastic energy during deformation.  $\beta = n_e / n$ and then *<sup>U</sup>*<sup>1</sup> <sup>=</sup> 0 and *<sup>U</sup>* <sup>=</sup> *<sup>O</sup>*("<sup>2</sup>  $\sigma$  and dissipation of energy in the fluid, while the imaginary part of the imaginary pa complex visit government the stored elastic energy during deformation. From Eq. (62), we have the stored elastic energy during definition. From Eq. (62), we have the stored elastic energy during deformation. From Eq. (62)  $\begin{array}{ccc} \vert -1 \vert & \vert & \vert \leq \end{array}$  =  $\vert k \vert \geq$  $\theta$ *r*  $\begin{array}{cccc} -2 & -1 & 0 & 1 & 2 \ \hline -2 & -1 & 0 & 1 & 2 \end{array}$ 2 1 0 *y* −1 ˆz *x*  $1 + \varepsilon f(\theta)$ 

along with orthonormal basis vectors,  $\mathcal{L}_\mathcal{A}$ 

$$
U = 2\varepsilon^2 \sum_{|k| \ge 1} \Re[\eta^*(k)] |\hat{f}_k|^2 J_k
$$
 Pumping is similar  
Confinement is similar

<sup>2</sup> dependencies in the *pumping* is similared  $\ln$  $f_k|^2 J_k$  Pumping is similar<br>Confinement is similar  $2J_k$  Pumping is similar<br>Confinement is sim

 $\sqrt{n}$ 

1 Fu, Powers & Wolgemuth, *Phys. Rev. Lett.*, 20<br>Leshansky *Phys. Rev. E*  $\frac{1}{2}$ 1 Eu, Wolgemuth & Powers, *Phys. Fluids*, 2009<br>Elfring *Phys. Fluids*, 2015 Li & Spagnolie, *Phys. Fluids*, 2015 Fu, Powers & Wolgemuth, *Phys. Rev. Lett.*, 2007 Leshansky, *Phys*<br>Fu Wolcemuth & Powers Phy v. Rev. E, 2009<br>8. Fluids 2009 Fu, Wolgemuth & Powers, *Phys. Fluids*, 2009<br>Elfring, *Phys. Fluids*, 2015 Li & Spagnolie, *Phys. Fluids*, 2015 pumping rate to *<sup>O</sup>*("<sup>2</sup>  $\left| k \right| \geq 1$  Lauga, *Phys. Fluids*, 2007,  $\begin{array}{c|c} -2 & -1 & 0 & 1 & 2 \end{array}$  Fu, Powers & Wolgemuth, *Phys. Rev. Lett.*, 2007<br> **Exhausky** *Phys. Rev. E.* 2009  $\frac{1}{x}$   $\frac{1}{x}$  Elfring, *Phys. Fluids*, 2015<br>Li & Spagnolie, *Phys. Fluids*, 2015 Li & Spagnolie, *Phys. Fluids*, 2015 in Stocker flow. This shows that the torque contributed by the torque contributed by the helical wave still enters as  $2015$ Leshansky, *Phys. Rev. E*, 2009



Spagnolie, Liu, & Powers, *Phys. Rev. Lett.*, 2013  $\alpha$  is  $\alpha$ ,  $\alpha$  is the peak of  $\alpha$  is suited. Stability of flagellum geometry to hoop stress (strangulation effect)...





Rod-climbing (McKinley Lab, MIT)

Flexible bodies? Multiple flagella? "Active suspensions"? Shear-thinning? Many questions remain open.



Yet other fluids are anisotropic (stress response is direction dependent) *a*<sup>*y*</sup>

Mucus and biofilms are anisotropic (in addition to viscoelastic, and shear-thinning…) **c** 



*b*

Boyer et al. Phys. Biol. (2011)

Cervical mucus



n?

Chretien (2003)



Filis in a nematic liquid crystal (DSCG) Mushenheim, Trivedi, Tuson, Weibel and *B. subtilis* in a nematic liquid crystal (DSCG)

subsett, Soft Matter, 2014. Abbott, Soft Matter, 2014. Mushenheim, Trivedi, Tuson, Weibel and **e f** Abbott, *Soft Matter*, 2014.

A nematic liquid crystal is a phase with **orientational order** but no positional order



Deviations from uniform alignment result in an **elastic** response…



 $\text{``Taylor's svrimminor sheet''}$  in a nema Legion & Swimming shoot in a home **Example 15**  $\cdot$  **"Taylor's swimming sheet" in a nematic liquid crystal**  $\overline{N}$ "Taylor's swimming sheet" in a nematic liquid crystal





Krieger, Spagnolie & Powers, (2014, 2015, 20. = !*t*, *v*⇤ = *v/c*, and *V* ⇤ = *V /c*, Krieger, Spagnolie & Powers, (2014, 2015, 2019)  $F111680,889$  plot of dimensionless swimming speed *U/(2011, 2010, 2010)* 

## Interesting new applications are just over the horizon…



### Performing useful work?



Urinary tract infections?

. Trivedi, Maeda, Abbott, Spagnolie & Weibel, *Soft Matter*, 2015 . Mushenheim, Pendery, Weibel, Spagnolie & Abbott, *PNAS*, 2017

Main points I wanted to highlight:

Physical ideas:

- 1. Kinematic reversibility / Scallop theorem
- 2. Quasi-static dynamics
- 3. Drag anisotropy of slender bodies
- 4. Stochastic (e.g. run-and-tumble) trajectories
- 5. Inside the flagellum: flagellin/polymorphism, microtubules/axoneme

Mathematical tools:

- 1. "Stokeslet" fundamental solution (Green's function) and its derivatives
- 2. A boundary-integral representation\*
- 3. Multipole expansion in the far-field: bacteria as force-dipoles.
- 4. Slender-body theory for thin filaments (flagella, cilia, etc.)

See also the following review articles:

Purcell, "**Life at Low Reynolds Number**", Am. J. Phys. (1977) Brennen & Winet, "**Fluid mechanics of propulsion by cilia and flagella**", Annu. Rev. Fluid Mech. (1977) Lighthill, "**Flagellar hydrodynamics**", SIAM Rev. (1976) Lauga & Powers, "**The hydrodynamics of swimming microorganisms**", Rep. Prog. Phys. (2009) Pak & Lauga, "**Theoretical models in low-Reynolds-number locomotion**" (2014)

<http://web.mit.edu/hml/ncfmf.html> And the classic video on Low Reynolds number flows from the National Committee for Fluid Mechanics Films:

**Authors**: Arratia, Brady, Caretta, Elfring, Evans, Ewoldt, Forest, Graham, Guy, Hatami-Marbini, Johnston, Kumar, Lauga, Levine, Mofrad, Morozov, Saintillan, Shelley, Spagnolie, Sznitman, Thomases, Vasquez, Zia

